Dendroecological detection of spruce bark beetle outbreaks in northwestern Colorado

Karen S. Eisenhart and Thomas T. Veblen

Abstract: Episodic outbreaks of *Dendroctonus rufipennis* (Kirby), the spruce bark beetle, have greatly influenced the structure of subalpine forests in northern Colorado. During the 1940s, much of the subalpine zone of northwestern Colorado was severely affected by beetle outbreak; also, tree-ring and photographic evidence suggest that large-scale outbreaks occurred in the 19th century. The present study focused on tree-ring methods to examine the regional extent and synchrony of pre-20th-century beetle outbreaks in northwestern Colorado. Results from examination of both live and dead Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) tree rings in nine stands were compared with results of previous tree-ring studies in the same region. Evidence of past canopy disturbance included episodes of tree mortality in conjunction with sustained increases in radial growth rates. We identified regional outbreaks of spruce beetle by synchronous and sustained growth release in trees from disjunct stands. These new tree-ring records, along with previously published records, indicate that severe and widespread canopy disturbances, probably spruce beetle outbreaks, affected northwestern Colorado in 1716–1750, 1827–1845, 1860–1870, and 1940–1960. These results support earlier findings that large-scale outbreaks of spruce beetle have long been an important component of the dynamics of subalpine forests in Colorado.

Résumé : Les épidémies périodiques de *Dendroctonus rufipennis* (Kirby), le dendroctone de l'épinette, ont grandement influencé la structure des forêts subalpines du nord du Colorado. La majeure partie de la zone subalpine du nord-ouest du Colorado a été sévèrement affectée par une épidémie du dendroctone durant les années 1940. Des indices photographiques et dendrochronologiques suggèrent que des épidémies importantes sont survenues au cours du 19e siècle. Cette étude met l'accent sur les méthodes dendrochronologiques pour étudier l'étendue régionale et la synchronicité des épidémies de l'insecte antérieures au 20e siècle dans le nord-ouest du Colorado. Les résultats de l'étude dendrochronologique d'épinettes d'Engelmann (*Picea engelmannii* Parry ex Engelm.) mortes et vivantes dans neuf peuplements ont été comparés aux résultats d'études dendrochronologiques antérieures dans la même région. Les indices de perturbations passées de la canopée incluaient des épisodes de mortalité des arbres parallèlement à des augmentations soutenues des taux de croissance radiale. Nous avons repéré les épidémies régionales du dendroctone de l'épinette grâce à des poussées de croissance synchrones et soutenues chez des arbres provenant de peuplements séparés. Ces nouvelles données dendrochronologiques, combinées à des données publiées précédemment, montrent que des perturbations sévères et très répandues de la canopée, probablement des épidémies du dendroctone de l'épinette, ont affecté le nord-ouest du Colorado de 1716 à 1750, de 1827 à 1845, de 1860 à 1870 et de 1940 à 1960. Ces résultats supportent les résultats antérieurs montrant que des épidémies très étendues du dendroctone de l'épinette sont depuis longtemps une composante importante de la dynamique des forêts subalpines du Colorado.

[Traduit par la Rédaction]

Introduction

The important agents of disturbance in subalpine forests of the southern Rocky Mountains, U.S.A., are wind, fire, and insect outbreaks (Peet 1981, 1988; Baker and Veblen 1990). Episodic outbreaks of *Dendroctonus rufipennis* (Kirby), the spruce bark beetle, are particularly widespread and are a major influence on the structure of subalpine forests in northern Colorado (Baker and Veblen 1990). For example, in the 1940s an outbreak of spruce beetle caused the mortality of >90% of the volume of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in White River National Forest

K.S. Eisenhart[1] and T.T. Veblen. Department of Geography, University of Colorado, Campus Box 260, Boulder, CO 80309, U.S.A.

[1]Corresponding author. e-mail: karen.eisenhart@colorado.edu

and moderate mortality in adjacent areas of northwestern Colorado (Hinds et al. 1965). Although prior studies have documented the occurrence of apparently widespread pre-20th-century outbreaks of spruce beetle in Colorado (Schmid and Frye 1977; Baker and Veblen 1990; Veblen et al. 1991b, 1991c), little is known about the regional extent and synchrony of these outbreaks. Knowledge of the frequency, extent, and timing of pre-20th-century outbreaks is important in assessing the potential for future spruce beetle outbreaks in this region. The present study uses tree rings to examine the history of spruce beetle outbreaks in the region of Routt National Forest, Colorado.

In northern Colorado, Engelmann spruce is the main host of spruce bark beetle. Endemic spruce beetle populations infest fallen trees and scattered live trees; however, following disturbance, abundant downed wood may provide a resource for endemic beetle populations to increase rapidly. These epidemic populations can then spread to live trees and may kill most canopy spruce over extensive areas (Schmid and Frye

Fig. 1. Map of northwestern Colorado showing the location of the study area in Routt National Forest and locations of sites sampled in the present study (the R and C sites), as well as other tree-ring sample sites discussed in the text (G and W sites; Veblen et al. 1991*a*).
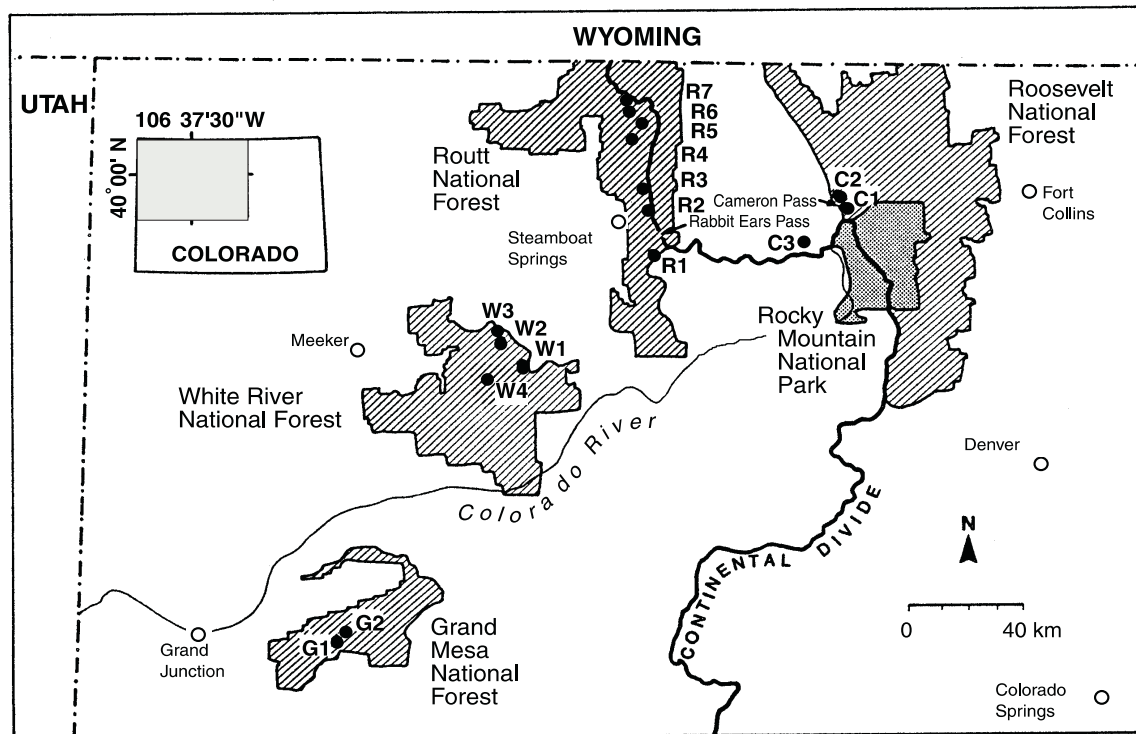
1977). Spruce beetles preferentially attack large-diameter trees. Spruce <10 cm in diameter are usually not attacked. During outbreaks, spruce beetle may attack and kill lodge-pole pine (*Pinus contorta* Dougl. ex Loud.) as well as spruce. Nearly all attacked trees are killed (Schmid and Frye 1977).

Tree rings have been used to detect past spruce beetle outbreaks by documenting episodes of synchronous mortality in host trees, and (or) by showing coincident growth releases of nonhost trees following the death of attacked trees (Veblen et al. 1991*b*, 1991*c*; Zhang et al. 1999). Radial growth of nonhost trees (i.e., nonhost species such as subalpine fir, *Abies lasiocarpa* (Hook) Nutt., and also small-diameter spruce) shows a persistent release (suddenly wider annual rings) lasting from a few years to well over 50 years. The intensity, duration, and spatial pattern of the release varies depending on the stand structure prior to beetle attack and the number of trees that are killed (Veblen et al. 1991*c*). Release is not precisely simultaneous, because hosts are not all attacked in the same year nor do they die in the same year. However, within stands of a few hectares in size, release is expected to occur within approximately 5 years of the initiation of beetle-caused mortality.

In the 1940s a beetle epidemic initiated following a blowdown in White River National Forest in Colorado in 1939 (Fig. 1). Mortality on the White River Plateau during that outbreak was the highest in the southern Rockies region in this century, but subalpine forests were also affected in other Colorado forests: Grand Mesa, Arapaho, Routt, San Juan, and Uncompahgre National Forests (Schmid and Hinds 1974; Schmid and Frye 1977; Baker and Veblen 1990). In Routt National Forest, the northern boundary of the outbreak

occurred near Buffalo Pass (Fig. 1, R2). Canopy trees in the Walton Creek area near Rabbit Ears Pass experienced approximately 40% mortality (Hinds et al. 1965). Although forests north of Buffalo Pass are also composed of Engelmann spruce and subalpine fir, it is not known why the 1940s outbreak did not spread into this area. Given the occurrence of a blowdown in 1997 in Routt National Forest, which affected 10 160 ha (Flaherty 2000) and increased the potential for spruce beetle outbreak (Schaupp et al. 1999), a longer term perspective on the extent and frequency of spruce beetle outbreaks is desirable.

Historical reports indicated widespread beetle damage to subalpine forests in Colorado in the late 1800s in the Pikes Peak region south of Denver (Hopkins 1909) and on the White River Plateau (Sudworth 1900). Following an outbreak, numerous dead-standing spruce trees signal the site of a beetle infestation, even after 50 years or more (Hinds et al. 1965). Thus, historical photographs from the late 1800s to 1900s that show a "salt and pepper" pattern of tree mortality suggest that spruce beetle outbreaks may have affected large areas of Colorado's subalpine zone (Baker and Veblen 1990; Veblen et al. 1994). In northern Colorado, tree-ring studies documented sustained and coincident growth releases suggesting widespread outbreaks in the early 1700s and middle to late 1800s (Miller 1970; Baker and Veblen 1990; Veblen et al. 1991*b*, 1994). However, the number of sites sampled to date is too small (<10) to establish the past extent and synchrony of outbreaks.

In this study we sampled spruce–fir stands within, and to the north of, the documented area of the 1940s outbreak in Routt National Forest (Fig. 1) with the following objectives:

Table 1. Summary data for site chronologies.

Site name	Site code	Elevation (m)	No. of cores cross-dated	Chronology period	No. of cores Live	Dead	Mean series correlation
Little Agnes Creek	R7	3010	22	1574–1997	22	0	0.635
Lost Dog Creek	R6	3020	20	1684–1996	19	1	0.535
Gold Creek	R5	2710	33	1549–1997	23	10	0.534
Big Creek Peak	R4	3120	13	1544–1997	12	1	0.670
Ribbon Forest	R3	3290	22	1563–1997	6	16	0.626
Buffalo Pass	R2	3100	54	1467–1997	17	37	0.661
Walton Creek	R1	3050	94[a]	1530–1986	18	76	0.605
Blue Lake Trail	C2	3020	95[a]	1437–1986	20	75	0.528
Illinois River	C3	2890	50	1480–1997	24	26	0.549

[a]Cores collected in a previous study were reanalyzed for the current project (Veblen et al. 1991a, 1991b, 1991c).

(*i*) to better describe the history of spruce beetle in the study area and (*ii*) to evaluate the regional synchrony of past outbreaks in northwestern Colorado. Trees were sampled from disjunct stands over a distance of 50 km. We also examined the instrumental climate record from nearby Steamboat Springs to determine if there was an abrupt shift in weather patterns that could have caused sudden and sustained increases in growth rate in some stands in this century. Correlation coefficients between tree growth and seasonal weather variables were used to document a similar growth response to seasonal temperature and precipitation among stands to permit comparison of radial increment among sites when the sample size is small. Knowledge of outbreak frequency and extent will be useful to forest managers and can be compared with reports of spruce bark beetle outbreaks in other parts of the southern Rocky Mountains.

Methods

Study area

The study area is located in northwestern Colorado (Fig. 1). Sampled stands were all spruce–fir stands located between 2710 and 3290 m in Routt National Forest or Roosevelt National Forest (Table 1). At this elevation the average time between frosts of 0°C is 46 days (Berry 1965), but frosts can occur at any time of the year. Precipitation is distributed fairly evenly throughout the year. Because of adequate precipitation and lower temperatures at these elevations, trees are generally not moisture stressed in most years.

Sample sites and field methods

Nine old (i.e., >200 years) spruce–fir stands in northwestern Colorado were sampled to investigate radial growth patterns (Table 1, Fig. 1). We selected sites following an extensive search for stands that showed potential beetle outbreaks. High-potential stands were located in well-drained creek bottoms and were composed of at least 65% large-diameter spruce (Schmid and Frye 1977). The presence of numerous dead-standing trees was considered indicative of beetle outbreaks in the recent past. Standing dead trees were evident at Walton Creek (R1), Buffalo Pass (R2), Ribbon Forest (R3), Gold Creek (R5), and Illinois River (C3). With the exception of Ribbon Forest (R3) and Big Creek Peak (R4), all sampled stands were located in creek bottoms. The following sites were located north of the limit of the 1940s beetle outbreak: Ribbon Forest (R3), Big Creek Peak (R4), Gold Creek (R5), Lost Dog Road (R6), and Little Agnes Creek (R7). Evidence of logging activity was absent from all sampled stands.

At sites C2, C3, R1, R2, and R3, two cores were collected from at least 20 spruce trees as low on the bole as possible (usually 30–

50 cm). Cores were taken from both live and dead trees, including a wide range of diameter sizes so that the signals in trees that released following the outbreak in the 1940s also would be sampled. (Table 1). Sites R4, R5, R6, and R7 were located within a recent (1997) large blowdown, and only one core was collected from at least 20 trees. In all sites, the largest trees were subjectively sampled, because previous research has shown that subjective samples yielded much longer, but otherwise similar, tree-ring records than did a random sample from the same area (Veblen et al. 1991b). If cores were partially rotten, they were kept if a cross-datable section of the sample was intact. When possible, dead trees were cored through the bark to reduce the probability of ring erosion and therefore to improve the precision of the estimated date of death. *Abies* were not sampled.

Samples were air-dried, mounted, and sanded with successively finer grades of sandpaper. Annual rings were counted under a stereomicroscope, and ring widths were measured to the nearest 0.01 mm with a slide-stage micrometer incremental measuring instrument. Cores from live trees were visually cross-dated using standard techniques (Stokes and Smiley 1968). The computer program COFECHA (Holmes 1983) was used to detect measurement and cross-dating errors by computing correlation coefficients between overlapping 50-year segments from individual series. If errors in cross dating could not be resolved the core was removed from the data set. Once live trees were cross-dated they were used to cross-date dead trees and determine the dates of their death. The percentage of trees that died in a given year was based on the number of samples alive during that year. Some trees may not have died in the year assigned because of weathering of outer rings or because of a few missing rings as the tree died; however, misdating of death by one to several years did not affect the interpretations in this study.

Tree-ring series from individual cores were inspected for growth releases by comparing consecutive groups of five rings. A growth release was defined in this study as a 200% increase in mean ring width between consecutive groups of 5 years. Thus, releases were identified by a change in relative ring widths but were not compared to the mean ring width of the entire series. Release data were summarized as the percentage of trees at one site that released in each year, based on the number of samples from that year.

Dendrochronological analyses

After experimenting with several methods of standardization, we determined that two different techniques were necessary for this analysis. In the first method, all cross-dated series were standardized by dividing each ring width by the mean series ring width. Standardizing series by their mean preserved the long-term growth trend used to identify canopy disturbance (Veblen et al. 1991b). Following standardization, the series were combined by site into master chronologies. Each chronology was visually inspected for

Table 2. Climate stations used to estimate missing values in the Steamboat Springs climate data set.

Station name	Station code[a]	Latitude (N)	Longitude (W)	Elevation (m)	Length of record	No. of months missing	
						Precipitation	Temperature
Fraser	53113	39°47′	105°50′	2609	1908–1975	26	120
Grand Lake 6SSW	53500	40°15′	105°50′	2554	1948–1997	11	38
Grand Lake 1NW	53496	40°16′	105°50′	2554	1939–1997	30	117
Green Mountain Dam	53592	39°53′	106°20′	2365	1939–1997	20	67
Hayden	53867	40°30′	107°15′	1932	1931–1997	12	65
Spicer 4NE	57848	40°29′	106°25′	2530	1931–1997	53	179
Steamboat Springs	57936	40°30′	106°50′	2063	1908–1997	29	159
Walden	58756	40°44′	106°16′	2469	1938–1997	22	57
Yampa	59265	40°09′	106°54′	2405	1941–1997	83	221

[a]Codes identify data sets associated with Colorado climate stations. Data source is the Colorado Climate Center at http://ulysses.atmos.colostate.edu

dramatic and sustained increases in growth rate that might indicate spruce beetle outbreak. Inclusion of younger, fast-growing trees in the same chronology with older, larger trees can potentially create the false impression of release. Therefore, we also plotted sample depth curves to consider the possible influence of a change in sample size on the form of the chronology curve. The magnitude of a release was compared only with the tree-ring indices that directly preceded the release and not to the whole chronology. Following individual site interpretation, chronologies were compared among sites to examine regional synchrony of canopy disturbances.

In the second standardization method, our goal was to develop mean chronologies in which interannual variability of growth could be related to year-to-year variation in precipitation and temperature. Consequently, in the second standardization method the long-term growth trend was removed by double-detrending each ring-width series. This involved fitting a negative exponential function or a trend line to each series of ring widths, followed by fitting a 100-year cubic spline to the detrended series. Following double detrending, an autoregressive function was applied to each series to remove serial autocorrelation and to enhance the common signal (program ARSTAN, Cook and Holmes 1986). The resulting residual series were averaged into a site chronology and regressed with seasonal weather variables to demonstrate that spruce–fir stands in the study area were responding similarly to weather.

Mean monthly temperature and total monthly precipitation data from Steamboat Springs, Colo. (elevation 2063 m), were used to determine the correlation of temperature and precipitation with interannual growth of spruce trees in the study area. The Steamboat Springs climate station is located near the study area to the west of the Continental Divide (Fig. 1) and is the longest continuous climate record for the region. Missing data in the Steamboat Springs record were estimated from eight nearby stations that had at least 50 years of climate information (Table 2). Most of the stations used to estimate missing data began data collection after 1930, and there are periods of missing or incomplete data in every record. Standard deviations from the monthly mean were calculated for stations with data points during the missing Steamboat Springs months. The departures for all stations were averaged and the average departure was applied to the Steamboat Springs monthly mean to estimate the missing value. Following estimation of all missing values in the Steamboat Springs record, the standard deviation of each month from the monthly mean was calculated for both mean monthly temperature and total monthly precipitation. Monthly temperature and precipitation deviations were averaged into seasons of 3 months beginning with February.

Correlation functions and response functions (Fritts 1976; Blasing et al. 1984) were used to relate variation in annual growth recorded by the residual chronology to seasonal weather variables. Because the resulting response functions determined with RESPO are considered unstable (Guiot 1991), we report only the correla-

tion coefficients of the first regression to show the response trend of tree growth to seasonal temperature and precipitation (Blasing et al. 1984). Fourteen variables were used in the analysis: seven 3-month seasons of departure data for temperature and precipitation, beginning with February–April (spring) of the previous growing season through August–October (fall) of the current growing season. Analysis begins with the previous growing season to identify a potential lag of correlation between tree growth and annual temperature or precipitation (Blasing et al. 1984).

The instrumental climate record was divided into two parts (1910–1945 and 1955–1997) to avoid the inclusion of the hypothesized release in growth caused by the widespread 1940s beetle outbreak. Correlation coefficients of tree growth with temperature and precipitation were determined for each sampled site during both halves of the instrumental record. Positive correlation suggests that above-average growth is correlated with an above-average value of the variable, whereas negative correlation suggests that above-average growth is correlated with a below-average value of a variable.

Results

Annual weather and tree growth

In this region, approximately equal amounts of precipitation fall throughout the year, but slightly more precipitation falls in winter than during the short growing season. Annual mean temperature has stayed within a single standard deviation of the long-term mean of 3.8°C, except for a record low annual temperature in 1924 (1.4°C) and two maxima in 1934 (6.2°C) and 1940 (5.6°C) (Fig. 2*a*). Seasonal precipitation is more variable from year-to-year (Fig. 2*b*). However, during this century, there has been no abrupt and long-lasting change in climate with which to confuse sustained growth release caused by beetle outbreak.

Within each of the two time periods analyzed (1910–1945 and 1955–1997), growth responses to seasonal temperature and precipitation variation were similar among the sites (Fig. 3). However, the general pattern of growth response differed slightly between the two time periods, even though a notable shift in year-to-year weather variation does not occur in the instrumental record. For the period from 1910–1945, growth of trees in Routt National Forest was most strongly correlated with below-average temperatures and above-average precipitation in the previous growing season (Fig. 3). A tendency towards negative correlation of growth with precipitation of the current spring at some of the higher elevation sites (e.g., R2) may reflect earlier snowmelt and, hence, a longer growing season. From 1955–1997, growth

Fig. 2. Time series showing temperature (broken line) and precipitation (solid line) departures from annual and growing season means at Steamboat Springs, Colorado from 1910 to 1997: (*a*) annual departures; (*b*) growing season departures (May–September). Departures are given in standard deviations from the mean.

(a) Annual

(b) Seasonal: May-September
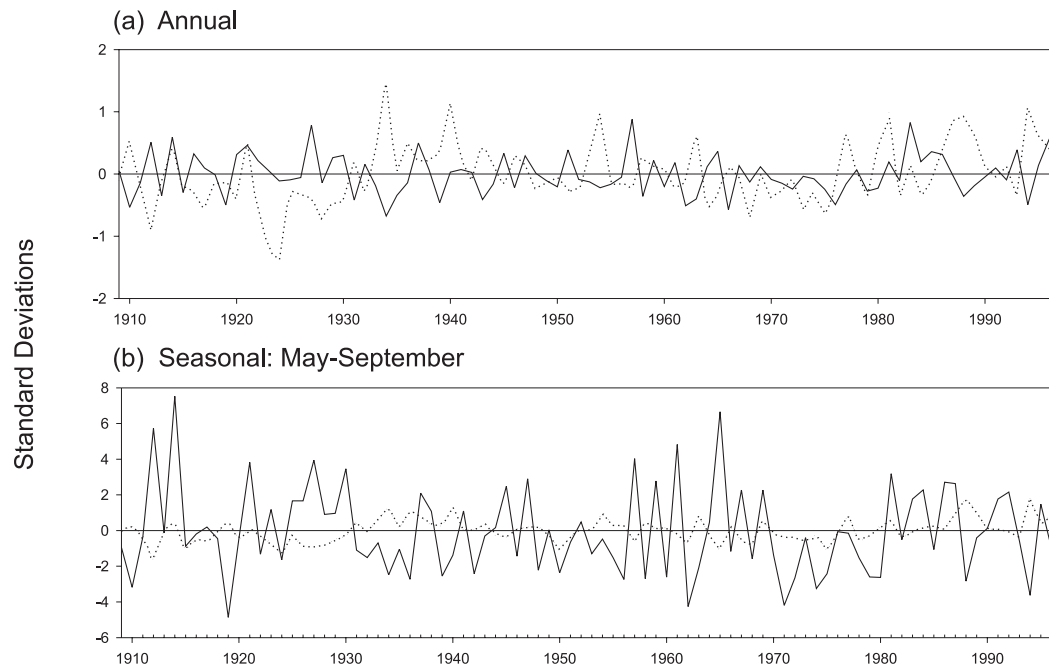
was most strongly correlated with below-average temperatures in the previous growing season, with high precipitation in the previous spring, and with warm temperatures during the current growing season (Fig. 3).

Overall, for the two time periods, growth is most consistently related to moisture availability during the previous growing season. Variation between the two time periods may reflect slight shifts in seasonality or the relatively minor differences in temperature or precipitation between the two time periods (Fig. 2). Despite these variations in the relationship of tree growth and climatic variation between the first and second halves of the 20th century, during the same time periods tree growth patterns were fairly consistent across sites. Because there is a similar growth response to seasonal weather among sites, major divergence of an individual site chronology from the regional pattern was assumed to indicate that a major disturbance affected that site rather than indicating site-specific differences in tree-growth response to regional climatic variation.

Stand-level disturbance histories

For all sites at least 75% of the collected cores were successfully cross-dated and consequently were included in the tree-ring analysis. Mean correlation of all cores with their master chronology was >0.5 (Table 1). Numbers of cores included in stand chronologies ranged from 13 to 95, and starting dates ranged from 1437 to 1684.

At Walton Creek (R1) the chronology indicates that releases began ca. 1585, 1740, 1830, and markedly ca. 1860 and 1946 (Fig. 4*a*). Sample size increases steeply between ca. 1745 and ca. 1850. A few trees died between 1850 and 1855, coincident with a high frequency of trees released ca. 1859. Sample size declines sharply ca. 1948, coincident with a 1950 peak in the chronology.

At Buffalo Pass (R2) the chronology indicates that releases begin ca. 1555, 1595, and especially 1850 (Fig. 4*b*). Sample size declines sharply in 1949, coincident with a peak in the chronology. Sample size increases steeply from ca. 1735 through 1840. A concurrent dip and sustained growth increment in the chronology during that time suggest a disturbance. Some mortality occurred ca. 1845, coincident with a high percentage of trees released.

Sample size and percent mortality at the Ribbon Forest (R3) show two recent episodes of mortality in 1948 and 1978 (Fig. 4*c*). Mortality in 1859 closely precedes a high frequency of trees that release ca. 1865. This release appears in the chronology but is preceded by an earlier period of release beginning ca. 1840. A release ca. 1770 is not strongly reflected by the chronology.

At Big Creek Peak (R4) the chronology indicates that releases began ca. 1595, 1715, and 1890 (Fig. 4*d*). The Gold Creek (R5) chronology clearly shows a release beginning in 1870 (Fig. 4*e*). A high frequency of trees released ca. 1760, 1772, 1833, 1874, and 1885 (Fig. 4*e*). The majority of mortality has occurred since 1980, with peak mortality in 1989. At Lost Dog Creek (R6), a number of releases indicated by high percentage of trees released began ca. 1785, 1840, 1879, and 1904–1915 (Fig. 4*f*). Two of these, 1785 and 1904, are indicated by the chronology, although generally the growth indices are in decline over the length of the record. At Little Agnes Valley (R7), there is no evidence of major canopy disturbance in the form of sustained releases in the chronology (Fig. 4*g*).

At Blue Lake Trail (C2), many trees died in the last 50 years but less synchronously than would be expected if mortality was caused by beetle outbreak (Fig. 4*h*). Clearly a disturbance occurred at this site ca. 1670, as evidenced by the chronology, an increase in sample size (i.e., tree establish-

Fig. 3. Correlations of growth response to precipitation and temperature, based on residual tree-ring chronologies and seven seasons of weather variables for 1910–1945 and 1955–1997. Positive correlations indicate that above-average tree growth is associated with above-average values of the weather variable. Negative correlations indicate that above-average tree growth is associated with below-average values of the weather variable. Previous (P) and current growing seasons (C) are indicated under the x axis. Seasons are spring (February–April), summer (May–July), fall (August–October), and winter (November–January).
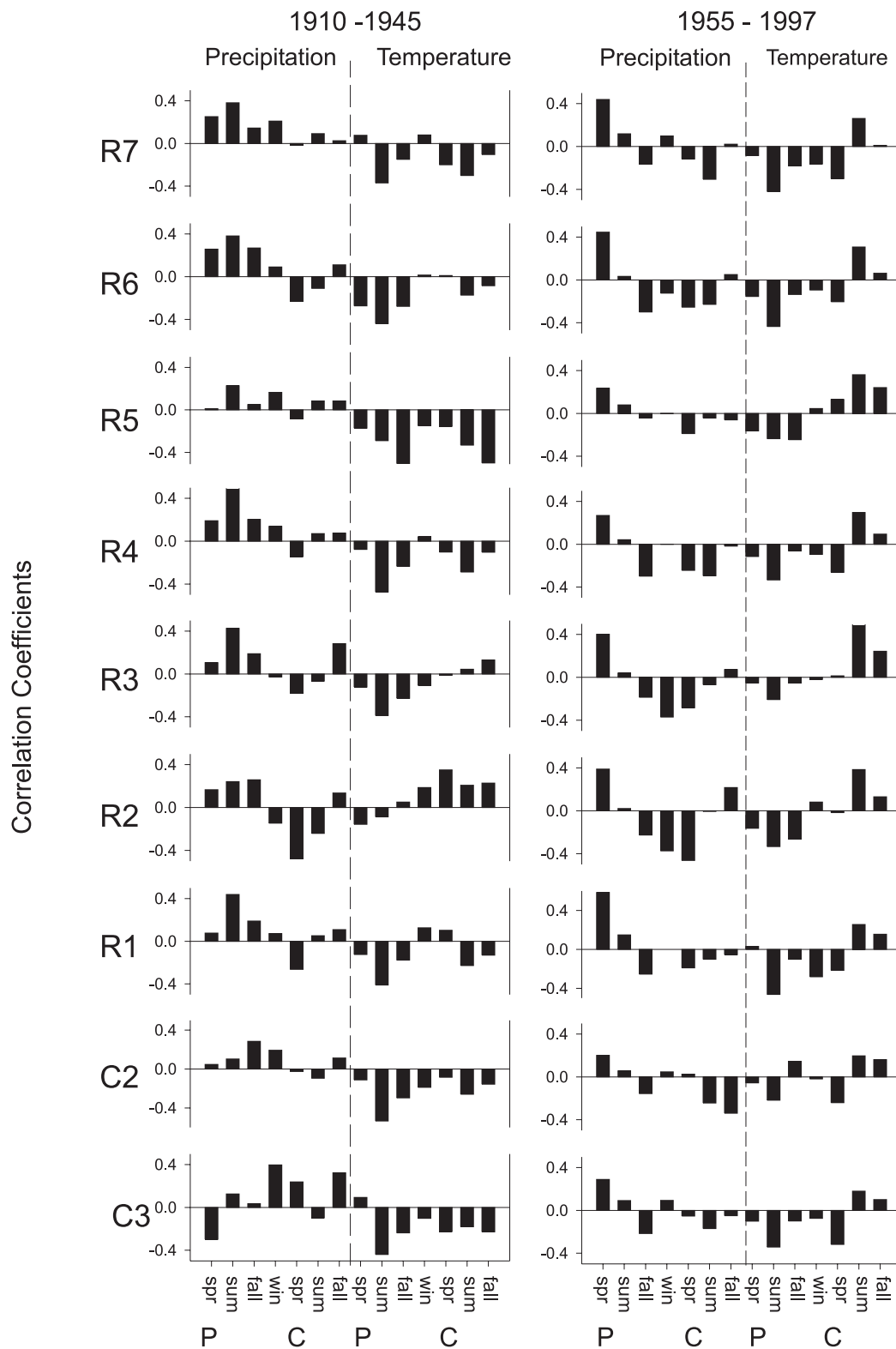
Fig. 4. Disturbance history by sampled site. Ring indices indicate site chronologies standardized by fitting a horizontal line through the mean of each series. The graph of *n* shows the number of cores in each chronology in each year. Percent mortality indicates the percentage of cores from trees that died in each year when compared with the total number of cores in the sample in that year. Percent release shows the percentage of cores in the sample with at least a 200% release in each year when adjacent groups of five rings are compared. Sites are (*a*) Walton Creek, R1; (*b*) Buffalo Pass, R2; (*c*) Ribbon Forest, R3; (*d*) Big Creek Peak, R4; (*e*) Gold Creek, R5; (*f*) Lost Dog Creek, R6; (*g*) Little Agnes Creek, R7; (*h*) Blue Lake Trail, C3; and (*i*) Illinois River, C2. At R4, release data is the number of trees with a >200% release. Few or no dead trees where sampled at sites R6 and R7, respectively.
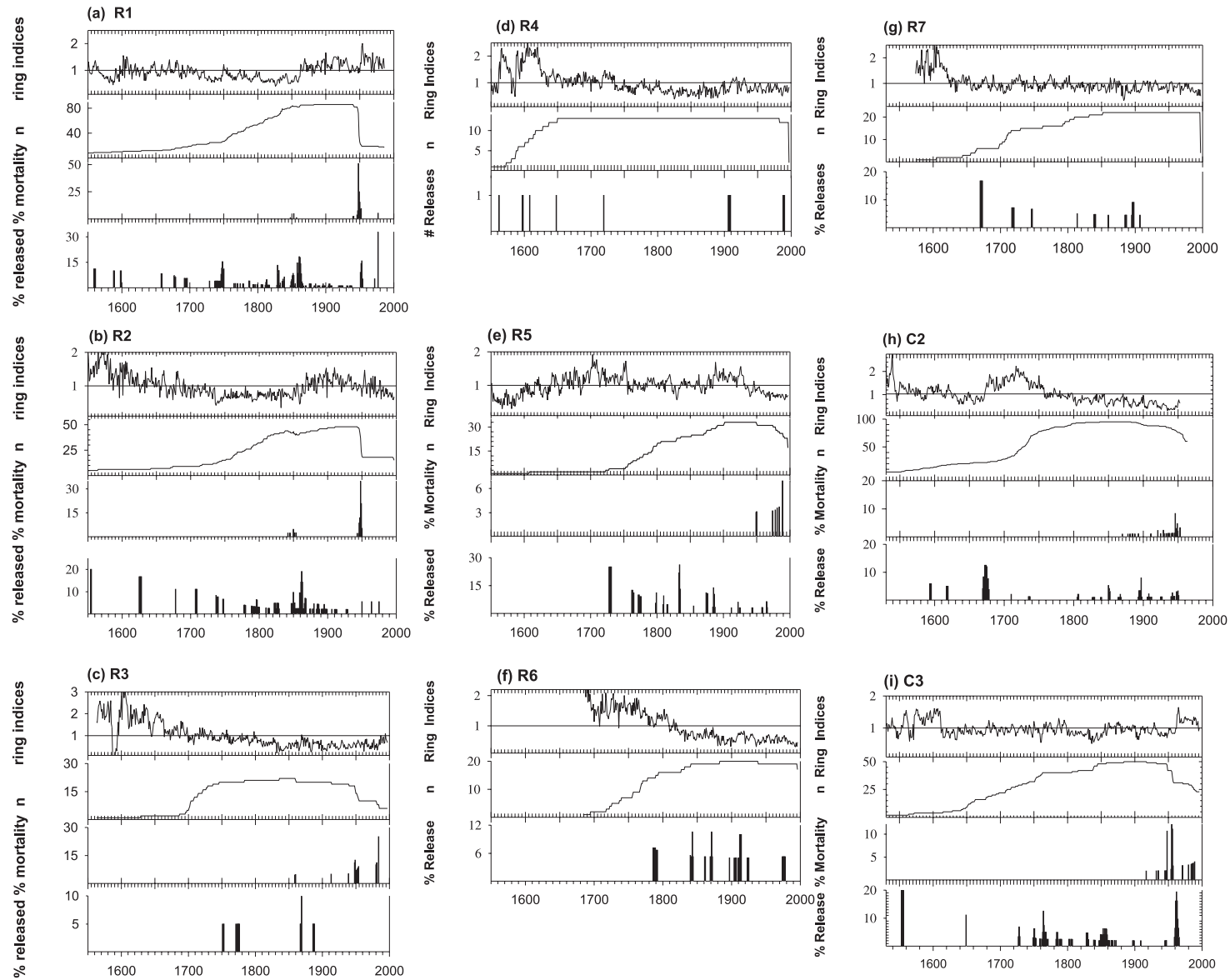
Fig. 5. Mean ring-width indices (standardized by the mean) for sampled sites. A broken vertical line indicates the date after which each chronology has $n \geq 5$ cores. For each site, an arrow above the time series indicates a canopy disturbance, possibly caused by spruce beetle outbreak. Canopy disturbance was inferred from evidence presented in Figs. 4 and 5 and Table 3.
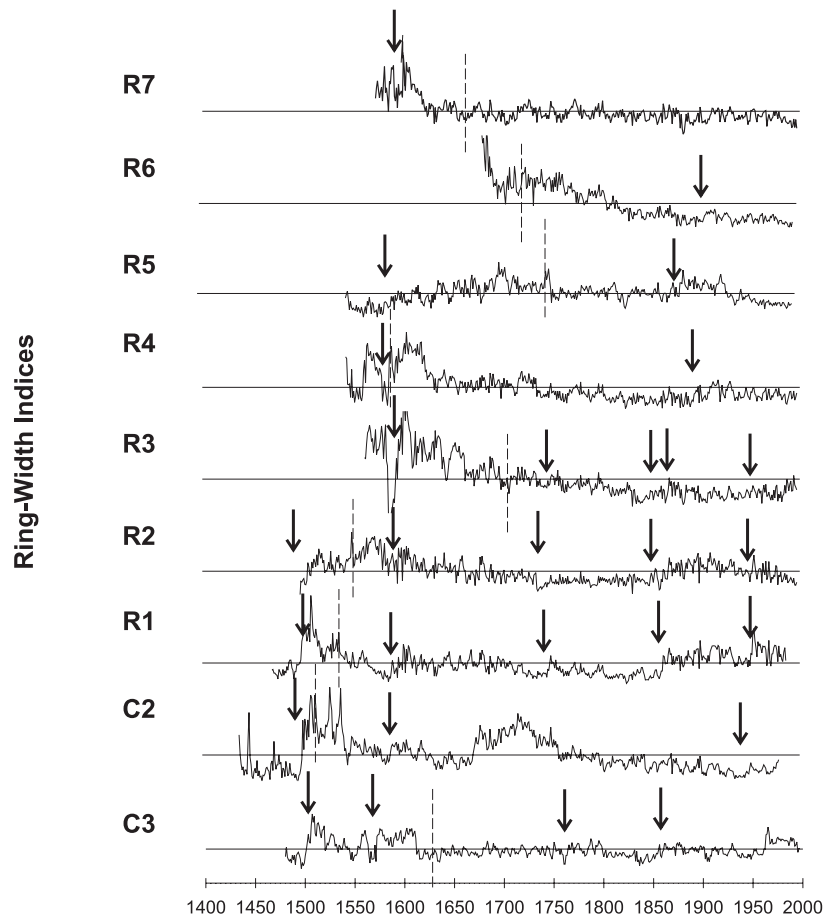
ment), and the percentage of trees released. A peak in mortality in 1946 is coincident with a spike in the chronology.

Dramatic and sustained release at Illinois River (C3) is shown by the chronology ca. 1960 (Fig. 4*i*). Release evident in the chronology and by a high percentage of trees with releases is coincident with high mortality from ca. 1946 to 1957. Sample size increases sharply ca. 1749–1761 and 1848–1860 and a high percentage of trees released between 1847–1857.

Regional synchrony of disturbance

Evaluation on a per-stand basis may detect only the most severe outbreaks, particularly prior to the late 1800s if no dead-standing trees have persisted to corroborate the interpretation that the release was caused by the death of canopy trees killed by beetles. However, when disturbance dates inferred from individual sites (Fig. 4) are compared (Fig. 5, Table 3), a pattern of synchronized canopy disturbances is evident. Synchronous canopy disturbance occurred in the middle to late 1800s (R5, R3, R2, R1, and C3) and the mid-1900s (R2, R1, C2) (Fig. 5). The 1960s release at C3 clearly occurs at least 10 years later than releases at R1 and R2 and, thus, is not considered part of a regionally synchronous canopy disturbance.

In the initial decades of long tree-ring chronologies when sample size is inevitably small, interpretation of releases is

difficult. Release of one or two trees early in the record of a site may represent competitive interactions affecting only those trees rather than a synchronous standwide release. However, if early releases are recorded simultaneously among several disjunct stands, even by small sample sizes, an exogenous cause is probable. Interpretation of the beginning of chronologies where sample size is <5 (Fig. 5) tentatively suggests that regional disturbance occurred ca. 1495 (R2, R1, C2, C3) and 1590 (in all except R6, where there is no data). Sample sizes are greater than five at sites R1, R2, and C2 during the late 16th century.

According to the criterion of the percentage of trees released each year (Fig. 5), severe regionwide canopy disturbances occurred in the middle to late 1800s in R1, R2, R5, and C3. R1 and R2 have an early episode of high percentages of released trees (ca. 1850) that coincides with releases at the Cameron Pass sites (C2 and C3). A second strong peak arises ca. 1860 in the two southern Routt National Forest sites (R1 and R2) and, to a much lesser extent, at R3 and after 1870 at R5. There is minor evidence of disturbance in the late 1800s at other Routt sites (R6 and R7). A less severe, but potentially regional event, is suggested by high percentages of released trees in the mid-1700s at C3 and R1, with low numbers of release during the same period at R7, R5, R3, and R2. Evidence of the 1940s outbreak is only recorded in the release data of trees from site R1 (Figs. 4

Table 3. Summary of initial year of a canopy disturbance inferred from interpretations at individual sites.

Source and site	Record	$(n \geq 5)^a$	Canopy disturbance dates									
This study												
Lost Dog Creek	R6	1726					1785	1840		1904		
Gold Creek	R5	1753					1760	1833	1870			
Big Creek Peak	R4	1588		1595		1715			1890			
Ribbon Forest	R3	1698					1770	1840	1865		1947	1979
Buffalo Pass	R2	1545	1555	1595		1735		1845	1860		1944	
Walton Creek	R1	1530		1585		1740		1830	1860		1945	
Blue Lake Trail	C2	1512			1670						1946	
Illinois River	C3	1615				1750		1840				1959
Veblen et al. 1991*b*, 1991*c*												
Cottonwood Lake	G1	1755						1845				1960
Big Creek Reservoir	G2	1765						1844			1940	1960
Trapper's Lake	W1	1869									1948	
Lily Pond	W2	1710									1945	
Ripple Creek	W3	1755					1795	1827			1945	
Veblen et al. 1994												
Marvine Lakes	W4	1650				1716		1827			1949	

^{a}Date after which each chronology has n ≥5 cores.

and 5). A canopy disturbance is indicated at C3 ca. 1960, but this outbreak has been identified as separate from the 1940s outbreak that began in the White River National Forest (McCambridge and Knight 1972).

Discussion and conclusions

We identified dates of potential spruce beetle outbreaks (Fig. 5, arrows) using the canopy disturbance dates from individual sites (Table 3), regional synchrony of disturbance (Fig. 5, Table 3), and synchrony of twofold or greater releases (Fig. 4). Evidence of all three types is only possible from the late 19th century to the present because of the decay and disappearance of trees that died in previous centuries. When only the tree-ring record is used to identify disturbance, the effect of beetle outbreak is difficult to distinguish from the effect of a blowdown. Historical observations of beetle-killed trees and historical photographs of dead-standing trees from the late 1800s were important for identifying outbreaks in the 19th century (Baker and Veblen 1990). However, for earlier time periods the distinction between blowdown and beetle outbreak must be inferred from less certain evidence such as the spatial distribution and composition of live and dead-standing trees, and the azimuths and species composition of fallen trees. For example, spruce beetle outbreaks are selective by species, whereas blowdowns affect all tree species. While dead-standing trees were noted in some plots (R1, R2, R3, R5, and C3), no plots contained evidence of old blowdowns. Where visual evidence of a blowdown or beetle outbreak has deteriorated and disappeared it may not be feasible to distinguish beetle disturbance from blowdown.

Alternative explanations for the observed patterns of growth releases include windstorms (not followed by beetle outbreaks), major outbreaks of other insects, or extreme weather events. All known spruce beetle outbreaks in Colorado have been initiated by blowdown. Where widespread blowdown was the source of beetle irruption, the two distur-

bances could certainly not be distinguished based on tree-ring records. However, blowdowns that affect disjunct stands over the full extent of the study area are rare. Therefore, it is possible that several stands could provide substrate for the initiation of a beetle outbreak, but it is unlikely that beetle outbreak and blowdown would be coincident in all stands. Consequently we feel that synchronous and sustained release across the study area is compelling evidence for a beetle outbreak. Bark beetles are the only insect known to cause widespread mortality to Engelmann spruce trees in the subalpine zone. Additionally, there is no precedent for widespread defoliation of subalpine fir by any insects. Therefore, it is unlikely that other insects are the cause of synchronous release.

Anomalous weather events (e.g., extreme cold or drought) may potentially have caused some of the observed growth releases. However, during the observational period for this region (after ca. 1890) we have been unable to find any reports of widespread tree mortality associated with temperature or precipitation anomalies. Indirectly, weather anomalies may have contributed to past spruce beetle outbreaks as reported for numerous other forest insect pests (Mattson and Haack 1987). Potentially, past droughts have contributed to spruce beetle outbreaks. For example, the three spruce beetle outbreaks at Marvine Lakes (site W4; Veblen et al. 1994) followed years of reduced growth in moisture-sensitive Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).

Based on the sites sampled in the current study, spruce beetle outbreaks appear to have occurred over a large part of the sampled area in ca. 1495, 1585, 1740, 1840, 1860, and 1945 (Fig. 5, Table 3). Canopy disturbance dates at Illinois River (C3), located at the southeastern border of the sample area, occurred in ca. 1570, 1760, and 1960 and are generally offset by at least 15 years from disturbance dates recorded at other sites. Dates of probable outbreaks from previously published studies for northwestern Colorado (Veblen et al. 1991*b*, 1991*c*, 1994) also indicate outbreaks in ca. 1716, 1827, 1845, and the 1940s (Table 3). Together, all these re-

cords indicate periods of widespread spruce beetle outbreaks in northwestern Colorado initiating in the years 1716–1750, 1827–1845, 1860–1870, and 1940–1960. The most recent two episodes of regional spruce beetle outbreaks are also documented by historical observation (Sudworth 1900; Schmid and Frye 1977) and historical photographs (Baker and Veblen 1990). Outbreak in the middle to late 1800s affected most of the stands in this study, with greater impact in the more southern stands (R1, R2, C2, and C3), but some release is apparent in all stands except the northernmost site (R7). Comparison of tree growth patterns at the more southern stands (R1, R2, C2, and C3) in the late 1860s and 1940s implies that the 1860s outbreak was more severe than the 1940s outbreak in the study area.

The 1940s outbreak was less severe in the Walton Creek area (Fig. 1, R1), than nearer to its source in the White River National Forest (Schmid and Frye 1977). Beetle disturbance in the 1940s, outlined on Forest Service maps, stops just north of the Buffalo Pass sample site (R2), with a few small patches of outbreak north of this area on the western side of the Continental Divide (USDA Forest Service 1949–1952). In most of the sample sites north of Buffalo Pass (R4, R5, R6, and R7), we did not find major sustained releases similar to those associated with higher percentages of beetle kill in the 1940s outbreak (Veblen et al. 1991*b*, 1991*c*, 1994). Although tree-growth patterns at sample sites north of the 1940s outbreak indicate some mild canopy disturbances in the mid-1800s that could be due to blowdown or low intensity spruce beetle outbreaks, we do not see evidence of massive canopy tree mortality indicative of an intense outbreak. However, this interpretation of a lack of past severe spruce beetle outbreak in the northern part of the study area must be tentative due to the relatively small number of sites sampled. Lack of major pre-20th-century spruce beetle outbreaks north of Buffalo Pass is consistent with the pattern of the 1940s outbreak.

This study found evidence of the 1940s outbreak at Walton Creek (R1) and at Buffalo Pass (R2), although at Buffalo Pass identification of the outbreak relied on the coincidence of death dates of dead-standing trees and appeared only as a small spike in the tree-ring chronology. Lack of signal in the tree-ring record at Buffalo Pass suggests that, where an outbreak is less intense (i.e., <40% mortality of canopy spruce), dates of host mortality are imperative for identifying the canopy disturbance as spruce bark beetle outbreak. Moderate release at C2 is also coincident with the 1940s outbreak, but the duration of increased mortality rates contrasts with the sharp peaks in mortality observed in beetle-attacked stands (contrast Figs. 4*a* and 4*h*).

Based on this study and previous reports (Schmid and Frye 1977; Baker and Veblen 1990; Veblen et al. 1991*c*), one or more outbreaks during the latter half of the 19th century appears to have affected a large proportion of the spruce–fir forests in the southern Rocky Mountains. At the scale of a small watershed (600 ha), the return interval of moderate to severe outbreaks was estimated at 117 years in the Marvine Lakes area of White River National Forest, located 80 km southwest of the present study area (Fig. 1; Veblen et al. 1994). According to the dates of outbreaks summarized here, at a regional scale in northwestern Colorado, exceptionally extensive and severe outbreaks (e.g., kill-

ing >90% of the canopy trees) may recur at intervals somewhat less than 100 years. However, outbreaks can recur to the same stands after just a few decades if prior outbreaks produced only limited mortality of susceptible trees (Schmid and Mata 1996). Following a massive episode of tree mortality, extensive regional outbreak may not recur until there are abundant, large-diameter spruce trees throughout subalpine canopies (Schmid and Frye 1977). Rates of canopy closure following an outbreak depend on site conditions and understory composition at the time of the outbreak, as well as the intensity of the outbreak. Widespread outbreak, as occurred in the 19th century, may only occur when many stands are in a similar and susceptible stage of development.

Widespread spruce beetle outbreaks prior to the 20th century predate any significant impacts from management activities such as logging or fire suppression in northern Colorado. In relation to the 1997 blowdown that affected 10 160 ha in Routt National Forest, there undoubtedly is an increased hazard of spruce beetle outbreak. However, it is useful for forest managers and the general public to know that large-scale tree mortality caused by insects has long been part of the natural dynamics of these forests.

Acknowledgements

References

Baker, W.L., and Veblen, T.T. 1990. Spruce beetles and fires in the nineteenth-century subalpine forests of western Colorado, USA. Arct. Alp. Res. **22**: 65–80.

Berry, J.W. 1965. Weathers of the states—Colorado. Weather Bureau, U.S. Department of Commerce, Washington, D.C.

Blasing, T.J., Solomon, A.M., Duvick, D. N. 1984. Response functions revisited. Tree-Ring Bull. **44**: 1–15.

Cook, E.R., and Holmes, R.L. 1986. Guide for computer program ARSTAN. *In* Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. *Edited by* R.L. Holmes, R.K. Adams, and H.C. Fritts. University of Arizona Press, Tucson. pp. 50–65.

Flaherty, P.H. 2000. Effects of pre-disturbance forest vegetation on the impacts of a catastrophic blowdown in a Rocky Mountain subalpine landscape. M.S. thesis, Department of Geography and Recreation, University of Wyoming, Laramie.

Fritts, H. 1976. Tree-rings and weather. Academic Press, London.

Guiot, J. 1991. The boot-strapped response function. Tree-Ring Bull. **51**: 39–41.

Hinds, T.E., Hawksworth, F.G., and Davidson, R.W. 1965. Beetle-killed Engelmann spruce. J. For. **63**: 536–542.

Holmes, R.L. 1983. Computer assisted quality control. Tree-Ring Bull. **43**: 69–78.

Hopkins, A.D. 1909. Practical information on the scolytid beetles of North American forests. I. Bark beetles of the genus *Dendroctonus*. U.S. Bureau of Entomology, Washington, D.C. Bull. 83. p. 169.

Mattson, W.J., and Haack, R.A. 1987. The role of drought in out-breaks of plant-eating insects. BioScience, **37**: 110–118.

McCambridge, W.F., and Knight, F.B. 1972. Factors affecting spruce beetles during a small outbreak. Ecology, **53**: 830–839.

Miller, P.C. 1970. Age distributions of spruce and fir in beetle-killed forests on the White River Plateau, Colorado. Am. Midl. Nat. **83**: 206–212.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range. Vegetatio, **45**: 3–75.

Peet, R.K. 1988. Forests of the Rocky Mountains. *In* North Ameri-can terrestrial vegetation. *Edited by* M.G. Barbour and W.D. Billings. Cambridge University Press, New York. pp. 46–101.

Schaupp, W.C., Frank, M., and Johnson, S. 1999. Evaluation of the spruce beetle in 1998 within the Routt Divide blowdown of Oc-tober 1997, on the Hahns Peak and Bears Ears Ranger Districts, Routt National Forest, Colorado. USDA Forest Service, Rocky Mountain Region, Lakewood, Colo. Biol. Eval. R2-99-08.

Schmid, J.M., and Frye, R.H. 1977. Spruce beetle in the Rockies. USDA For. Serv. Gen. Tech. Rep. RM-49.

Schmid, J.M., and Hinds, T.E. 1974. Development of spruce–fir stands following spruce beetle outbreaks. USDA For. Serv. Res. Pap. RM-131.

Schmid, J.M., and Mata, S.A. 1996. Natural variability of specific forest insect populations and their associated effects in Colo-rado. USDA For. Serv. Gen. Tech. Rep. RM-275.

Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree ring dating. University of Chicago Press, Chicago, Ill.

Sudworth, G.B. 1900. White River Plateau Timber Land Reserve. *In* Twentieth annual report of the United States Geological Sur-vey, Part V: forest reserves. U.S. Geological Survey, Washing-ton, D.C. pp. 117–179.

USDA Forest Service. 1949–1952. Map: Engelmann Spruce Bark Beetle Control Project, Arapaho, White River and Routt Na-tional Forests. USDA Forest Service, Denver, Colo.

Veblen, T.T., Hadley, K.S., and Reid, M.S. 1991*a*. Disturbance and stand development of a Colorado subalpine forest. J. Biogeogr. **18**: 707–716.

Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1991*b*. Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests. Can. J. For. Res. **21**: 242–254.

Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1991*c*. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology, **72**: 213–231.

Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., and Villalba, R. 1994. Disturbance regimes and disturbance interac-tions in a Rocky Mountain subalpine forest. J. Ecol. **82**: 125–135.

Zhang, Q., Alfaro, R.I., and Hebda, R.J. 1999. Dendroecological stud-ies of tree growth, weather and spruce beetle outbreaks in central British Columbia, Canada. For. Ecol. Manage. **121**: 215–225.